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ARTICLE

Scale and strength of oak–mesophyte interactions in a transitional oak–hickory forest

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Abstract: Forests in eastern North America are undergoing rapid compositional changes as they experience novel climate, disturbance, and pest conditions. One striking pattern is the replacement of canopy oaks (*Quercus* spp.) by mesic, fire-sensitive, shade-tolerant species like red maple (*Acer rubrum* L.). To gain insight into the successional patterns driving stand-level canopy oak replacement, we ask two questions: (*i*) What is the spatial association of oak and mesophyte recruitment compared with oak and mesophyte overstory individuals, and (*ii*) How do oaks and mesophytes differentially respond to canopy openings. We analyzed census data from a 23 ha forest plot surveyed in 2003, 2008, and 2014. We show that oak recruits are negatively associated with overstory red maples and black cherries (*Prunus serotina* Ehrh.), whereas mesophytic recruits were positively associated with overstory oaks. Second, we found that proximity to a dead overstory tree increased growth and survival for black cherries, increased growth for red maples, but had no effect on oaks. Black cherries and red maples are therefore better suited than oaks to take advantage of canopy openings and the moderate light available under adult oaks. These same fine scale competitive processes are contributing to canopy oak replacement across eastern North America.

Key words: oak replacement, succession, pair correlation function, red maple, mesophication.

Résumé : Les forêts de l'est de l'Amérique du Nord subissent des changements rapides de composition en raison de nouvelles conditions concernant le climat, les perturbations et les ravageurs. Un exemple frappant est le remplacement des chênes (*Quercus* spp.) du couvert dominant par des espèces mésiques, sensibles au feu et tolérantes à l'ombre comme l'érable rouge (*Acer rubrum* L.). Pour mieux comprendre les schémas de succession menant au remplacement du chêne dans le couvert dominant des peuplements, nous posons deux questions : (*i*) quelle est l'association spatiale du recrutement du chêne et des mésophytes comparativement aux individus des mêmes espèces présents dans le couvert dominant? et (*ii*) quelles sont les différences de réaction des chênes et des mésophytes face aux ouvertures du couvert? Nous avons analysé les données d'inventaire d'une parcelle forestière de 23 ha mesurée en 2003, 2008 et 2014. Nous montrons que les recrues de chêne sont négativement associées aux érables rouges et aux cerisiers tardifs (*Prunus serotina* Ehrh.) de l'étage dominant alors que les recrues mésophytiques sont positivement associées aux chênes du couvert dominant. De plus, nous avons constaté que la proximité d'un arbre mort dans le couvert dominant augmentait la croissance et la survie des cerisiers tardifs et augmentait la croissance des érables rouges, mais n'avait aucun effet sur les chênes. Les cerisiers tardifs et les érables rouges s'acclimatent donc mieux que les chênes pour tirer profit des ouvertures du couvert et de la disponibilité modérée de la lumière sous des chênes adultes. Ces mêmes processus concurrentiels à petite échelle contribuent au remplacement du chêne dans le couvert dominant des forêts de l'est de l'Amérique du Nord. [Traduit par la Rédaction]

Mots-clés : remplacement du chêne, succession, fonction de corrélation densité-densité, érable rouge, mésophisation.

Introduction

Hardwood forests across eastern North America are experiencing rapid shifts in species composition associated with changes in climate, disturbance regimes, and land use, as well as changes in pest, pathogen, and herbivore populations. The effects of these changes have been particularly striking in oak-dominated stands (Abrams 1996). Since the 1930s, elevated mortality of large oaks coupled with limited oak recruitment has resulted in a decline in their role as canopy dominant species (McEwan et al. 2011). Over the last 30 years, this trend has been observed in most oak species and most regions in the eastern United States (Fei et al. 2011). An understanding of this canopy oak loss and the resulting changes

to stand composition will inform a discussion of the future of oak-dominated forests and their management.

The exact mechanism for this canopy oak replacement is debated (McEwan et al. 2011). One hypothesis attributes the oak loss to decreased drought severity, suggesting that it has facilitated the recruitment of drought-sensitive, shade-tolerant species, which in turn have displaced oaks from the understory (Pederson et al. 2015). Another hypothesis proposes that fire suppression has provided fire-sensitive, shade-tolerant species, e.g., red maple (*Acer rubrum* L.), with a competitive advantage over oaks (Nowacki and Abrams 2008, 2015). This could lead to a process of mesophication, a positive feedback between mesophytic species and the abiotic

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conditions these species both favor and cause (Nowacki and Abrams 2008). The increased abundance of shade-tolerant, drought- and fire-sensitive species limits light availability in the understory because of their higher leaf area. Heavier shade decreases the temperature and wind speed on the forest floor and increases the relative humidity. These abiotic changes reduce the susceptibility of the stand to fire, which create a positive feedback further favoring mesophytic species.

There is support for this putative positive feedback. Juvenile red oaks grow slower and have lower survival in low light environments than juvenile red maples and other mesophytic species (Pacala et al. 1996). Furthermore, although light is generally the limiting resource for red oak sapling growth, soil moisture can be a limiting resource for red maples and sugar maples (*Acer saccharum* Marsh.) (Kobe 2006). Therefore, if forest floors become darker and wetter, maple regeneration should be favored over oak. Once the process starts, dense understory mesophytes are then a major obstacle to oak seedling growth and survival (Lorimer et al. 1994). Experimental evidence supports this conclusion. Iverson et al. (2008) report that prescribed thinning and burning favored oak recruitment over maple and that oak recruitment was the greatest in areas of high light and xeric conditions. Finally, evidence comes from oak-dominated stands across eastern North America in which recruitment histories were reconstructed. These studies found continuous oak recruitment prior to the early 20th century, which was largely replaced by mesophyte recruitment thereafter (Abrams and Copenheaver 1999; Abrams et al. 1995; Hart et al. 2012; Hutchinson et al. 2008; Shumway et al. 2001). In a subset of these studies, the fire history of the stand was also reconstructed, and fires were frequent during the period of oak recruitment, although they were rare or absent during subsequent mesophyte recruitment (Hutchinson et al. 2008; McEwan et al. 2007; Shumway et al. 2001).

Although the underlying drivers of mesophication have been characterized, there are still gaps in our knowledge of stand-level oak–mesophyte interactions. First, as mesophytes replace oaks in the canopy, we need to understand how oak and mesophyte recruitment patterns respond to canopy changes. One way to do that is by measuring the species-specific spatial association between recruits and overstory individuals (Cowell et al. 2010; McDonald et al. 2003). Here, we present a better way to measure those associations through non-cumulative spatial statistics and comparison with a null dispersal model. Second, as canopy gaps form, we need to understand how oak and mesophyte survival and growth differentially respond. Here, we measure these species-specific responses with data from a large forest dynamics plot that has been censused three times.

This study was conducted in a 23 ha research plot in a transitional oak–hickory forest in southeast Michigan. The plot was censused three times over an 11-year period. The most recent census captured >45 000 stems ≥1 cm diameter at breast height (DBH, 1.3 m). We used the census data to address these questions: (*i*) What is the spatial association between the overstory *A. rubrum*, *P. serotina*, and *Quercus* spp. and recruits of these taxonomic groups; and (*ii*) How does the growth and mortality of individuals of each of these three groups respond to the death of a neighboring overstory tree?

Methods

Site and data collection

This study was conducted at the Big Woods plot within the University of Michigan's Edwin S. George Reserve in Pinckney, MI (42°27′24.36″N, 84°00′40.03″W). The plot has steep moraine and basin topography and is dissected by a large esker. Upland portions have well-drained sandy loam or loamy sand soils, whereas portions below 275 m elevation have soils of organic deposits and muck. Oaks and hickories dominate the forest overstory. The oaks

are predominantly white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), and Hawkins' oak (*Q.* × *hawkinsiae* Sudw. [*rubra* × *velutina*]). The hickories are pignut (*Carya glabra*), shagbark (*C. ovata*), and bitternut hickory (*C. cordiformis*). The overstory (trees ≥20 cm DBH) is 36% red oak group (*Quercus* section *Lobatae*), 20% white oaks, 16% hickories, 14% black cherries (*Prunus serotina* Ehrh.), 10% red maples (*A. rubrum*), and less than 4% remaining species. The mid- and sub-canopy (trees <20 cm DBH) are 32% witch-hazel (*Hamamelis virginiana* L.), 21% black cherry, 16% red maple, and less than 2% each oaks and hickories. See Allen et al. (2009) for more description of the forest.

Historical pre-settlement vegetation reconstructions suggest a large fraction of what is now the George Reserve was covered by black oak barren, mixed oak forest, wet prairie, and mixed hardwood swamp (Comer et al. 1995). The Big Woods plot area was likely largely covered by black oak barren and mixed oak forest. Kost et al. (2007) described southern Michigan's black oak barrens and oak-dominated dry forests as fire-dependent communities. This suggests the region could have had a history of fire prior to European settlement, although we do not have a documented fire history of the George Reserve. The current forest composition of oak–hickory canopy and red maple – black cherry understory does not have a historical analogue, as Dodge (1987) found that red maple and black cherry were not common in the pre-settlement oak forests of southcentral Michigan. Dodge (1987) also suggests that the rise in importance of these species is related to fire suppression. This history is also supported by the abundance of large red maples in the swamps and along wetland borders, which would have had some protection against ground fires.

The Big Woods plot was originally set up in 2003 as a 12 ha plot with all individuals larger than 10 cm circumference (= 3.2 cm DBH) identified, measured, and mapped. This plot was re-censused in 2008 and an additional 11 ha were added. In 2014, the full 23 ha plot was re-censused and individuals down to 1 cm DBH were added, following the protocols of the Forest Global Earth Observatory network (ForestGEO) (Condit 1998), of which the Big Woods plot is now a member (available from http://www.forestgeo.si.edu/).

For the following analyses, all oak species were grouped together and compared with the dominant mid-canopy mesophytic species, red maple and black cherry. The results were largely unchanged when the analyses were conducted separately on white oaks and oaks in the red oak section (*Q.* section *Lobatae*).

Statistics

Recruitment

We measured the spatial association between overstory trees for each group and the recruits of each group with an inhomogeneous bivariate pair correlation function (PCF). The PCF, $g(r)$, is the density of points in a ring of radius r around a focal point divided by the average density of those points (Velázquez et al. 2016). The bivariate version measures the spatial association of points of two different types, so it measures the density of type A points around focal points of type B divided by the average density of type A points. In either the bivariate or univariate case, the PCF is preferable to the more commonly used Ripley's K because it is non-cumulative (Perry et al. 2006; Velázquez et al. 2016). In cumulative spatial statistics, the value of that statistic at radius r is the cumulative effect from 0 to r, rather than the effect just at r. This makes it hard to interpret the true scale of an association. We used the inhomogeneous PCF because none of the point patterns was homogenous across the plot. See Velázquez et al. (2016) for a discussion of the importance of using inhomogeneous spatial statistics.

We defined recruits as individuals that were too small to be included in the 2008 survey (<3.2 cm DBH) but large enough to be included in the 2014 census (≥3.2 cm DBH). We defined overstory trees as those with a DBH of at least 20 cm. We calculated nine

bivariate inhomogeneous PCFs, one measuring the spatial association of each taxonomic group's recruits to each group's overstory individuals. The taxonomic groups were red maple, black cherry, and all oaks.

We compared each PCF with the expected PCF under a null dispersal model in which recruits were randomly dispersed from adult individuals of that group. The null dispersal models were based on species-specific dispersal functions from Martin and Canham (2010). For each group, the same number of recruits as observed were randomly attributed to adults based on species-specific DBH–recruits produced relationships from Martin and Canham (2010). These recruits were then "dispersed" in a random direction from that adult with distance drawn from species-specific lognormal dispersal kernels, also taken from Martin and Canham (2010). They gave these functions for black cherry, red maple, and red oaks. The red oak DBH–recruits produced relationship and dispersal kernel were used for our oak group. We ran the null dispersal model 100 times for each taxonomic group. The result of each random recruit placement was then compared with the actual spatial pattern of overstory individuals for the three groups with a bivariate inhomogeneous PCF. We created 95% confidence intervals of these PCF values. This allowed us to compare the actual spatial arrangement of recruits with the expectation if their arrangement was derived solely from dispersal from adult individuals. This analysis was done with the spatstat package in R (Baddeley and Turner 2005; R Core Team 2017).

Proximity to dead overstory tree

We tested the effect of being within 10 m of a tree larger than 20 cm DBH that died between 2003–2008 on the growth and mortality of individuals between 2008 and 2014. We took 20 cm DBH as the cut-off for overstory trees. We had to restrict this analysis to individuals in the original 12 ha of the plot, as those are the only ones for which we had the 2003 census data. The growth and mortality response was measured separately for black cherries, red maples, and oaks. The species of the dead overstory tree was not considered.

We modeled average annual DBH growth from 2008 to 2014 as a lognormal function of 2008 DBH. The lognormal function has the flexibility of taking many empirically observed shapes with a low number of parameters (Uriarte et al. 2004),

$$(1) \qquad \text{DBH growth} = g_i \exp\left[-0.5\log\left(\frac{(\text{DBH}/\mu_i)^2}{\sigma_i}\right)\right]$$

where $i = 1$ for individuals within 10 m of an overstory tree that died between 2003 and 2008, and $i = 2$ for individuals farther than 10 m for such a tree. Parameters g_i, μ_i, and σ_i determined the shape of the lognormal growth function. We fit this separately for each species. We then fit a simpler version of the model in which $g_1 = g_2$, $\mu_1 = \mu_2$, and $\sigma_1 = \sigma_2$. In other words, for each species, we fit two models: one in which the DBH–growth relationship is different for individuals within 10 m of a dead overstory tree and those that are not, and a second model in which all individuals have the same DBH–growth relationship. The second simpler model is nested within the full model, so we compared them with the likelihood ratio test (Bolker 2008). If the more complex model fit significantly better, we could say that proximity to a dead overstory tree had an effect on tree growth for that species. This analysis was done in R with the package bbmle (Bolker 2017; R Core Team 2017).

We took a similar approach to measuring how proximity to a dead tree affected mortality. We modeled the probability of mortality between 2008 and 2014 as an exponential function of 2008 DBH. In some cases, tree mortality is U-shaped with tree size (Lines et al. 2010). However, for our three groups, mortality decreased

with size, so we used an up-shifted exponential function for the DBH–mortality relationship:

$$(2) \qquad P(\text{mortality}) = a_i \exp(-b_i\text{DBH}) + c_i$$

where $i = 1$ for individuals within 10 m of an overstory tree that died between 2003 and 2008, and $i = 2$ for individuals farther than 10 m for such a tree. Parameters a_i, b_i, and c_i determined the shape of the exponential mortality function. We fit this model separately for each species and then for each species a simpler version where $a_1 = a_2$, $b_1 = b_2$, and $c_1 = c_2$. The two models were compared with the likelihood ratio test. This analysis was done in R with the package bbmle (Bolker 2017; R Core Team 2017).

Results

Recruitment

Recruitment was highly uneven among the three groups. Between 2008 and 2014 over the 23 ha plot, there were 244 black cherries, 295 red maples, and 32 oaks that recruited into the ≥3.2 cm DBH size class. Figure 1 shows the results from the PCF analysis, which measures the spatial association between recruits and overstory individuals. Take Fig. 1C as an example; it shows the association between black cherry recruits and overstory oaks. The black line shows the actual data. When the PCF, $g(r)$, is greater than one, there were more black cherry recruits than average black cherry recruit density r meters away from overstory oaks. For example, $g(2.5 \text{ m}) \approx 1.5$ means that 2.5 m away from the average overstory oak, there are 1.5 times more black cherry recruits than the average overall density of black cherry recruits. The gray bands show the expected results under the null black cherry dispersal model. At all scales between 0 and 20 m, there were more black cherry recruits around overstory oaks than the average black cherry recruit density (>1) and there were more than expected by the black cherry dispersal model (above the gray band). This effect was strongest at small spatial scales (<2 m).

Overall, from this analysis, we can see that there are fewer recruits found close to conspecifics than expected under the dispersal model (Figs. 1A, 1E, and 1I). For black cherries (Fig. 1A) and oaks (Fig. 1I), this was significant at 0–2.5 m, whereas for red maples, it was significant at 0–20 m.

For interspecific interactions, we see that both black cherry and red maple recruits were positively associated with overstory oaks (Figs. 1C and 1F). The effect was strongest between 0 and 5 m, but it was significant for all spatial scales considered. Oak recruitment was negatively associated with overstory black cherries at all spatial scales considered (Fig. 1G). However, oak recruitment was not as affected by overstory red maples (Fig. 1H). Between 0 and 3 m, oak recruits' association with overstory red maples was no different from that expected under the null oak dispersal model. At spatial scales farther than 3 m, there was only a marginally significant reduction in oak recruit density with overstory red maples.

Proximity to dead overstory trees

Between 2003 and 2008, 113 overstory trees died. For both black cherry ($\chi^2 = 12.7$, df = 3, $p = 0.005$) and red maple ($\chi^2 = 37.4$, df = 3, $p = 3.8 \times 10^{-8}$), the more complicated model, which included proximity to dead overstory tree, fit better than the simpler model. Thus, for those two species, individuals within 10 m of a dead overstory tree had a significantly different DBH–growth relationship than those farther than 10 m of a dead overstory tree. In both cases, those individuals grew faster (Figs. 2A and 2B). The fit curves show that for red maple, this difference was greatest for individuals of ~10–15 cm DBH, whereas for black cherry, the difference increased with the size of the tree. On the other hand, there was no significant difference in growth for oaks based on proximity to dead overstory tree ($\chi^2 = 5.6$, df = 3, $p = 0.13$; Fig. 2C). This means that although black cherry and red maple individuals were able to

Fig. 1. The bivariate inhomogeneous pair correlation functions (PCF) measuring the spatial association of recruits to overstory, >20 cm DBH, trees. The analysis is separated by taxonomic group, with the recruit groups in rows and the overstory groups in columns. The PCF value, $g(r)$, is the density of recruits in rings of radius r (meters) around overstory individuals divided by the expected density of recruits. The black solid lines show the data and gray intervals show the 95% expectation under the assumption that recruitment patterns are solely the result of dispersal from adults.
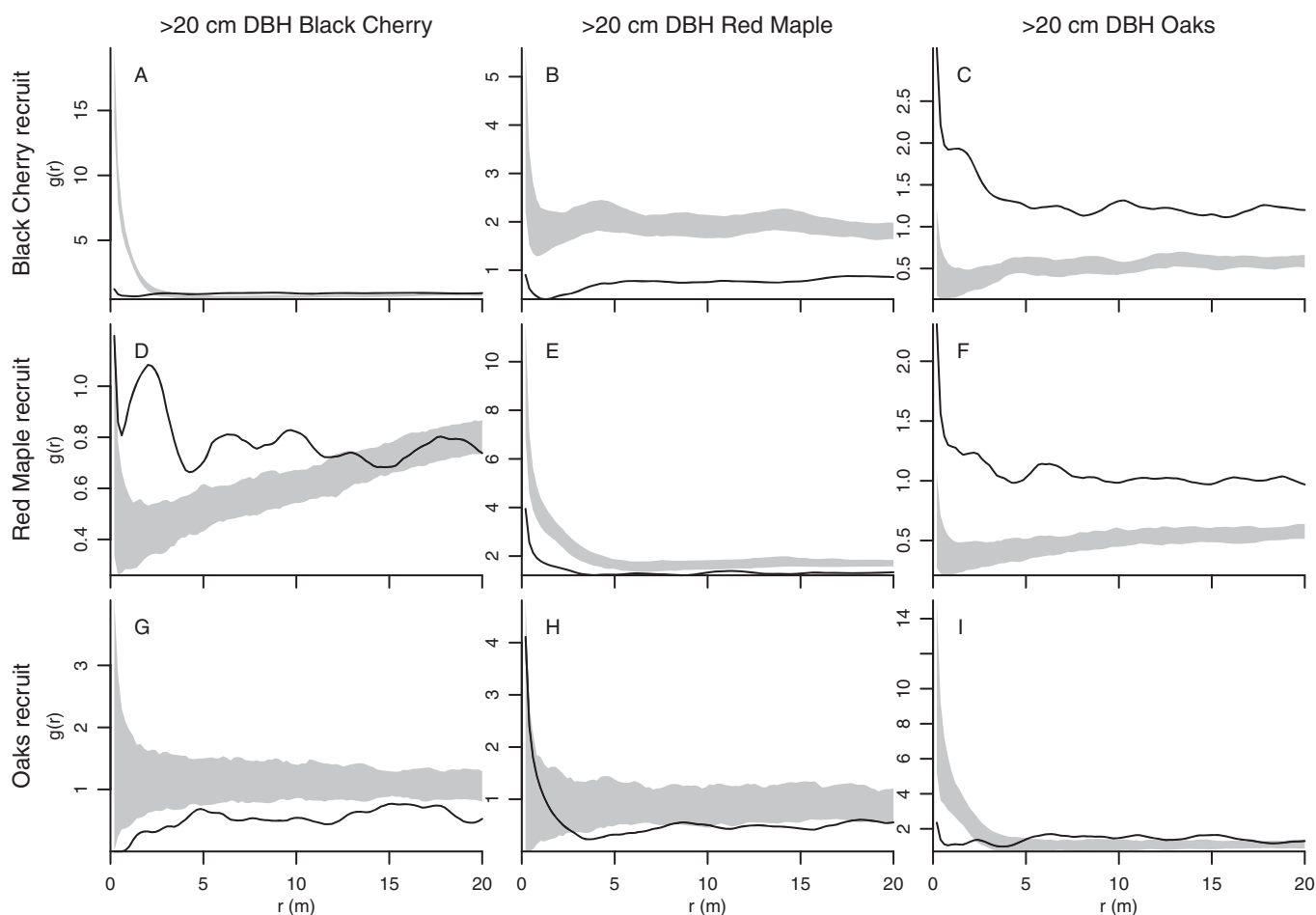
take advantage of canopy openings with faster growth, oaks were not.

For mortality, we found a similar pattern for black cherries. For that species, the more complicated model that included proximity to dead overstory tree fit better than the simpler model ($\chi^2 = 11.6$, df = 3, $p = 0.009$). There was a reduction in 2008–2014 mortality for black cherries within 10 m of an overstory tree that died between 2003 and 2008. This reduction was most pronounced for individuals less than 10 cm DBH (Fig. 3A). On the other hand, the model that included proximity to a dead tree did not do a significantly better job describing red maple ($\chi^2 = 4.7$, df = 3, $p = 0.20$) or oak ($\chi^2 = 4.8$, df = 3, $p = 0.19$) mortality. For those individuals, the single model performed just as well at describing mortality (Figs. 3B and 3C).

Discussion

In this study, we measured stand-level oak–mesophyte interactions in a forest experiencing mesophyte replacement of canopy oaks. Although other studies (Cowell et al. 2010; McDonald et al. 2003) have measured the spatial association between oak and mesophyte recruitment compared with overstory trees, we were better able to interpret the spatial scale of that association with a non-cumulative spatial statistic. We were also able to measure the differential response of oaks and mesophytes to canopy openings. With three censuses of the same forest plot, we used the first to

second census to identify canopy tree deaths and then second to third census to measure the response of surrounding trees to those deaths (and the light gaps produced).

Previous studies have measured the spatial association of oak recruitment and overstory or midstory density (Cowell et al. 2010; McDonald et al. 2003). These studies use Ripley's K to show a negative association between mid-canopy density and oak recruitment at very large spatial scales (>20 m). However, Ripley's K is a cumulative spatial statistic, so the value at a given scale, r, is the cumulative value between 0 and r distance. Thus, it is hard to tell whether a measured association at distance r is due to a process that truly has an effect at r distance away or from the cumulative effect at shorter distances (Perry et al. 2006). Here, we are able to measure the association at each distance using the non-cumulative PCF.

These results show that oak recruitment is negatively associated with proximity to both overstory black cherries and red maples, although the effect of the black cherry is stronger. McDonald et al. (2003) also found that oak recruitment was negatively associated with adult red maples, but they did not look at black cherries. Presumably, the main reason for this negative association is that red maple and black cherry canopies block more light than oak canopies do (Pacala et al. 1996), and thus, there is less oak recruitment under the deeper shade of the mesophyte canopy. It may also be that areas of higher overstory black cherry and red maple density have dense midstories of those species as well and

Fig. 2. Relationship between 2008 DBH and average annual DBH growth from 2008 to 2014. For each group, we compared two models: one model fit separately for individuals within 10 m of a dead overstory tree and those farther; and a second simpler model that fit the same relationship for all individuals. For black cherry and red maple, the more complex model fit better, whereas for oaks, the simpler model did just as well. For black cherry and red maple, the dotted line is the model fit for trees within 10 m of a dead overstory tree and the solid line is for those farther. For oaks, the single fit relationship is shown. We show binned data rather than all data points for easier interpretation. For each species, we binned individuals into deciles based on 2008 DBH and then calculated the average growth and DBH for each bin. Error bars indicate the standard error of growth for each bin. We do this separately for individuals within 10 m of a dead tree (exes, x) and those farther (open circles, o). Note different axis scales for each subgraph: (A) black cherry, (B) red maple, and (C) oaks.
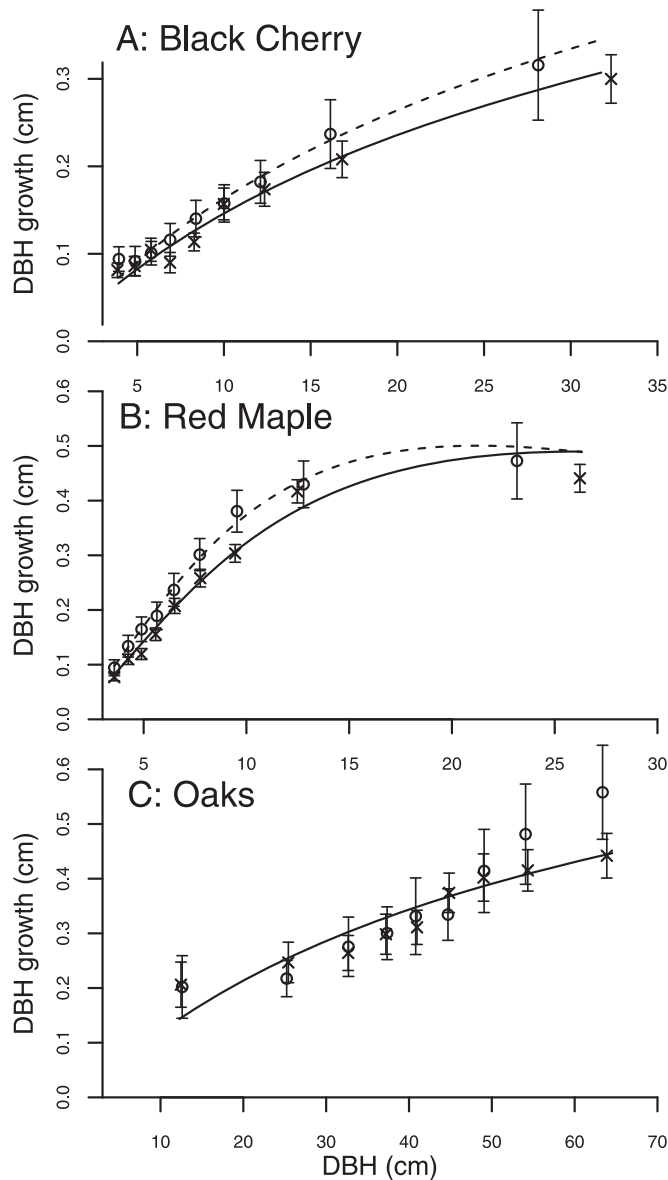
Fig. 3. Relationship between 2008 DBH and 2008–2014 mortality. For each species, we compared two models: one model fit separately for individuals within 10 m of a dead overstory tree and those farther; and a second simpler model that fit the same relationship for all individuals. For black cherry, the more complex model fit better, whereas for red maple and oaks, the simpler model did just as well. For black cherry, the dotted line is the model fit for trees within 10 m of a dead overstory tree and the solid line is for those farther. For red maple and oaks, the single fit relationship is shown. We show binned data rather than all data points for easier interpretation. For each species, we binned individuals into septiles based on 2008 DBH and then calculated the average mortality and DBH for each bin. Error bars indicate the standard error of mortality for each bin. We do this separately for individuals within 10 m of a dead tree (exes, x) and those farther (open circles, o). Note different axis scales for each subgraph: (A) black cherry, (B) red maple, and (C) oaks.
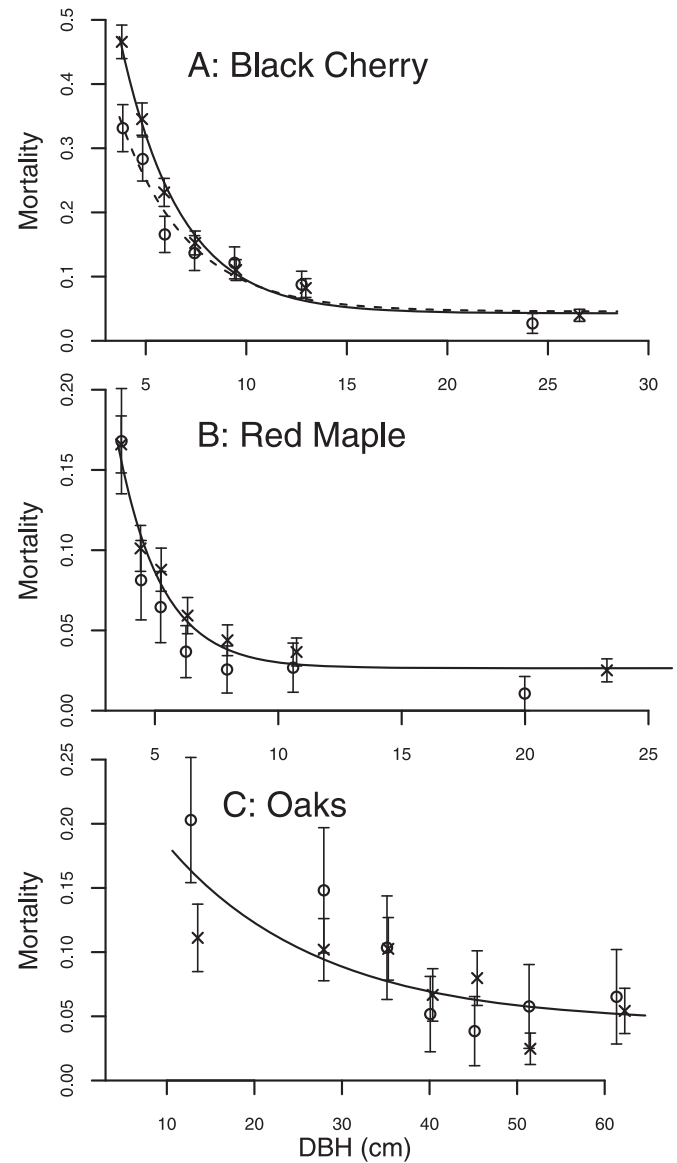
that it is those midstory individuals that are directly affecting oak recruitment. Lorimer et al. (1994) found that the shade of a dense mesophyte midstory decreases oak seedling growth and survivorship.

However, neither of these would explain the negative association we see at larger spatial scales (>5 m). This perhaps is a result of subtle edaphic factors. Canopy-sized red maples and black cherries are found more commonly in mesic sites, whereas oak recruitment is generally limited to more xeric locations (Iverson et al.

2008). Thus the negative association between mesophyte over-story individuals and oak recruits at larger spatial scales could be the result of this difference in soil water requirements. Although we did not measure any soil characteristics, we do, anecdotally, note that the largest black cherry and red maple individuals are restricted to mesic sites near ponds and swamps, whereas oak recruitment is largely limited to more xeric sites with sandy soils and a thick *Vaccinium* ground cover. This pattern of oak regeneration limited to the xeric sites has been noted in other oak-dominated forests (Hart and Kupfer 2011; McEwan and Muller 2006).

The PCF analysis also showed a negative association between the overstory individuals and conspecific recruits of each group. This pattern is to be expected if there is Janzen–Connell density-dependent recruitment limitation (Connell 1971; Janzen 1970). This recruitment limitation was proposed as a mechanism for high levels of diversity in tropical forests (Janzen 1970) and has been observed in many tropical species (Harms et al. 2000). However, it has also been observed in several temperate forest species (Hille Ris Lambers et al. 2002). Previous studies have documented recruitment farther from adult trees than expected by seed rain in black cherry, red maple, and red oak (Hille Ris Lambers and Clark 2003; Packer and Clay 2000). We found an especially strong pattern of negative density dependence for black cherry, which could be the result of the soil pathogen *Pythium* spp. (Packer and Clay 2000).

In the second part of our study, we found that mesophytes responded positively to the death of an overstory tree, whereas oaks did not. Previous studies have used gap-capture methods to predict which individual would capture a gap in oak-dominated forests (Taylor and Lorimer 2003; Richards and Hart 2011). These studies find that even in forests where oaks dominate the canopy, gap capture is expected to be accomplished by non-oak, shade-tolerant mesophytes. Here, we provide support and a possible explanation for these predictions. Black cherry individuals near dead overstory trees showed faster growth and higher survival and red maples individuals showed faster growth; however, oaks did not show a response.

Shade-tolerant species often require multiple episodes of release and suppression before reaching the canopy (Canham 1985, 1990). However, canopy oak trees were most likely to have originated in an opening and reach the canopy before canopy closure (Rentch et al. 2003). Again, our result helps to explain this finding; the small amount of additional light from one dead canopy tree did not provide enough resources for a release event for oaks as it did for the mesophytes. Based on personal observations, most of these canopy openings were relatively small. This suggests that they are more likely to be closed by lateral expansion rather than subcanopy recruitment (Richards and Hart 2011; Weber et al. 2014). Overtopped subcanopy mesophytes may not fully capture the gap, but the opening may provide enough of an increase in growth to make them better able to take advantage of future gaps.

We found differences between how the two mesophytic species responded to these canopy openings. For black cherry individuals, the largest increase in size with proximity to canopy opening was for the largest DBH trees. These faster growing large black cherries may then capture the canopy opening by lateral expansion, though we did not predict canopy capture in this study. On the other hand, 10–20 cm DBH red maples had the largest increase in size with proximity to canopy opening. Canham et al. (2006) found that 15 cm DBH red maples responded more strongly to crowding, whereas larger ones are less sensitive. As the canopy opening forms and preferentially supports the growth of mid-canopy red maples, this could in turn further decrease oak recruitment (Lorimer et al. 1994).

There was also a difference in how canopy openings affected the mortality of red maples and black cherries. Although red maple mortality did not change with proximity to a canopy opening,

black cherry mortality decreased. This decrease in mortality was especially large for black cherry individuals less than 10 cm DBH, which otherwise had a high mortality rate. This decrease in mortality was probably due to an increase in light availability, as black cherry saplings have relatively high mortality at low light levels (Kobe et al. 1995).

There is a general consensus that burning is required to maintain oak dominance in stands undergoing mesophication (Arthur et al. 2012). In a meta-analysis of 32 studies in mixed-oak forests, Brose et al. (2013) found that prescribed fire can reduce midstory stem density and preferentially select for oak over mesophyte reproduction. However, they caution that single fire treatments were generally not enough and that multiple burns were needed to benefit oaks in the long term. Iverson et al. (2017) further suggest that an initial partial harvest was needed before the first burn to promote oak regrowth. They also found that even with thinning and three burns over 13 years, mesophyte recruitment is favored over oaks in mesic sites. As a result, they recommend that burning is only worth the cost on xeric sites. Our study does not directly test fire regimes but generally supports these recommendations. We found that red maples and black cherries are better able to capture natural canopy gaps than oaks. Fires have been shown to control midcanopy mesophytes (Brose et al. 2013), which could allow oak capture of natural canopy gaps. Our results also support the recommendation that fire is only recommended for certain oak sites (Iverson et al. 2017). We found that oak recruitment is greatly reduced with proximity to canopy mesophytes, but Arthur et al. (2012) note that large red maples survive prescribed burns. Thus, in mesic areas with existing mesophytic canopies, burning treatments may not support enough oak rather than mesophyte recruitment to be worth the cost.

The patterns found here are consistent with the basic pattern of oak replacement by more shade-tolerant species. These results were possible to measure in a forest research plot that has been sampled three times over the last 11 years. Much work has been done on research plots in old-growth forests to study processes and patterns at equilibrium. Here, we highlight the importance of plots in transitional forests to give better insights into successional processes.

Acknowledgements

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